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SHORT COMMUNICATION

Habitat use, non-breeding groupings and chromatic pattern in *Johngarthia lagostoma* (H. Milne Edwards, 1837) (Decapoda, Gecarcinidae) in Trindade Island, South Atlantic Ocean

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Abstract
The land crab *Johngarthia lagostoma* is endemic to Trindade Island, Atol das Rocas, Fernando de Noronha and Ascension Islands. The natural history of the species in non-breeding periods is little known. Therefore, here we reported the formation of non-breeding groups and evaluated the chromatic populational pattern of *J. lagostoma* in Trindade Island. Records were obtained between April and June 2015. The groups were characterized according to their location, terrain elevation, environmental characteristics and specimens' behavior. The chromatic pattern was defined by the classification of individuals between yellow and purple, and the proportion of each color was compared between populational units (previously defined based on genetic differences). Non-breeding groups were recorded in four locations in Trindade Island, at altitudes < 40 m, and all of them were in locations with food resources and sediment suitable for the construction of shelters. Isolated individuals or the absence of the species were observed in the most inhospitable places, indicating that the maintenance of the species depends on portions of suitable habitat amid the currently arid matrix. Yellow individuals (96.4%) were predominant on Trindade Island and the chromatic pattern differed from the other populations. Color patterns seem to follow genetic differences between populations, and the founder effect may account for current patterns. From the data obtained, we emphasize that the maintenance of the species may depend on food, sediment suitable for shelters construction, humidity and shade. Due to the significant population decline

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in other regions, the need to define guidelines for the conservation of the species on Trindade Island is highlighted. In this context, the regeneration of insular vegetation and prohibiting the known anthropic consumption of individuals may represent important strategies for the maintenance of the species.

Keywords
Chromatic variation, founder effect, insular environment, land crab, natural history, oceanic islands

Introduction

The land crab, *Johngarthia lagostoma* (H. Milne Edwards, 1837), occurs in the South Atlantic and is endemic to the Brazilian archipelagos of Trindade, Fernando de Noronha and Atol das Rocas, and to the British island of Ascension (Pinheiro et al. 2016). The carapace width of this crab is about 90 mm and the individuals show a chromatic variation between yellow/orange and purple (Hartnoll et al. 2006; João et al. 2021). Few individuals show intermediate coloration, being predominantly yellow with purple patches on the carapace (Hartnoll et al. 2006). Adults reside in the interior of the islands, associated with terrestrial vegetation, and reproduction depends on the marine environment (Hartnoll et al. 2010). The reproductive period occurs seasonally, between December and May (Southern Hemisphere summer), as observed on Ascension Island (Hartnoll et al. 2010), Atol das Rocas (Teixeira 1996) and Trindade Island (João et al. 2021). In the reproductive period, individuals migrate to the coast in large groups composed mainly of females, which enter in the water and release the larvae from eggs previously fertilized in the terrestrial environment (Hartnoll et al. 2010). The larvae have pelagic development (Cuesta et al. 2007) and, after this stage, the juvenile individuals return to the coast and migrate to the interior of the islands, where they remain during the adult stage (Hartnoll et al. 2006; Hartnoll et al. 2014).

The species has a generalist diet and, due to its complex life cycle, participates at different levels of the trophic chain, acting as prey during the marine larval stage and as a top predator in terrestrial environments when adults (Lira 2017). By intensely preying on eggs and hatchlings of seabirds and sea turtles, *J. lagostoma* contributes to animal populations' control and participates in the dispersion of nutrients between marine environments and terrestrial insular ecosystems (e.g., Oliveira 2021). Furthermore, for consuming plant material (e.g., Hartnoll et al. 2006), the species participates in the cycling of this type of matter and in the control of plant populations. Thus, the species can be considered important for the maintenance of the island ecosystem.

In Brazil, *J. lagostoma* occurs in less than 5,000 km^2, with an evident reduction in its original occupied area, for example, in Fernando de Noronha due to urban growth (Santana and Coelho 2018). Currently, the species is classified as Endangered, with the loss of habitat, the presence of invasive species (Santana and Coelho 2018) and the illegal consumption of individuals as the main threats (Serafini et al. 2010). Genetic differences divide the species into three populational units, one comprising Atol das Rocas and Fernando de Noronha, the other occurring on Trindade

Island and the last on Ascension Island (Rodríguez-Rey et al. 2016). This highlights that the conservation of every populational unit is important for the maintenance of the genetic variability of the species. Although most populations are located in Brazil, studies on *J. lagostoma* are scarce in the country (e.g., Teixeira 1996; Lira 2017; Oliveira 2021), and detailed information on the biology and use of the habitat is restricted to Ascension Island (e.g., Hartnoll et al. 2006; Hartnoll et al. 2009). Furthermore, there is no detailed information about the behavior of the species in the non-breeding periods.

Here we aim to report the formation of non-breeding groups, provide information on habitat use and evaluated the chromatic populational pattern of *J. lagostoma* in Trindade Island, providing subsidies for its conservation.

Methods

Study area

Trindade Island is located 1,200 km from Vitória (Espírito Santo state), in southeastern Brazil (Fig. 1), and is inserted in the Atlantic Forest Biosphere Reserve (RBMA 2021). It has an area of 9.28 km^2 and has an extremely rugged relief, reaching 620 m of elevation (Alves 1998). Trindade Island is the only Brazilian oceanic island to have perennial streams (Marques et al. 2019). The climate in the region is considered tropical oceanic, with an average annual rainfall of 923 mm (Marques et al. 2019). In the past, the island was dominated by *Colubrina glandulosa* Perkins forest (~ 85% of the island; Alves 1998), but with human occupation, in around 1700, herbivorous mammals (e.g., goats, pigs and sheep) and other domestic animals were introduced, resulting in the suppression of native vegetation (Alves 1998). As a result, there was total soil exposure in many locations, reduction in water availability and intensified erosion, causing the loss of most of the island's organic soil (Alves 1998). Currently, Trindade Island presents arid landscapes with vegetation composed by grasses, and a cloud forest occupies the highest elevations (> 400 m; Alves 1998; Fig. 1).

Habitat use

Records of *J. lagostoma* were obtained by non-systematized sampling (visualization of the specimens from non-predefined transects) between April 3 and June 20, 2015. During this period, most of the altitudinal ranges (including some peaks of the higher regions), and different environments were sampled, including most of the perimeter of the island (rocky and sandy beaches), water courses, herbaceous fields, cloud forest and buildings ("Posto Oceanográfico da Ilha da Trindade" – POIT, Trindade Island Oceanographic Outpost). The sampled places were accessed by trails, with the most remote beaches (western portion) accessed by sea with the aid of a boat (Fig. 1). Records were characterized qualitatively, giving special attention to agglomerations (groups) of individuals. The groups consisted of detecting at least 10 individuals together, with the specimens visually close from the other individual (Fig. 2). Information about the loca-

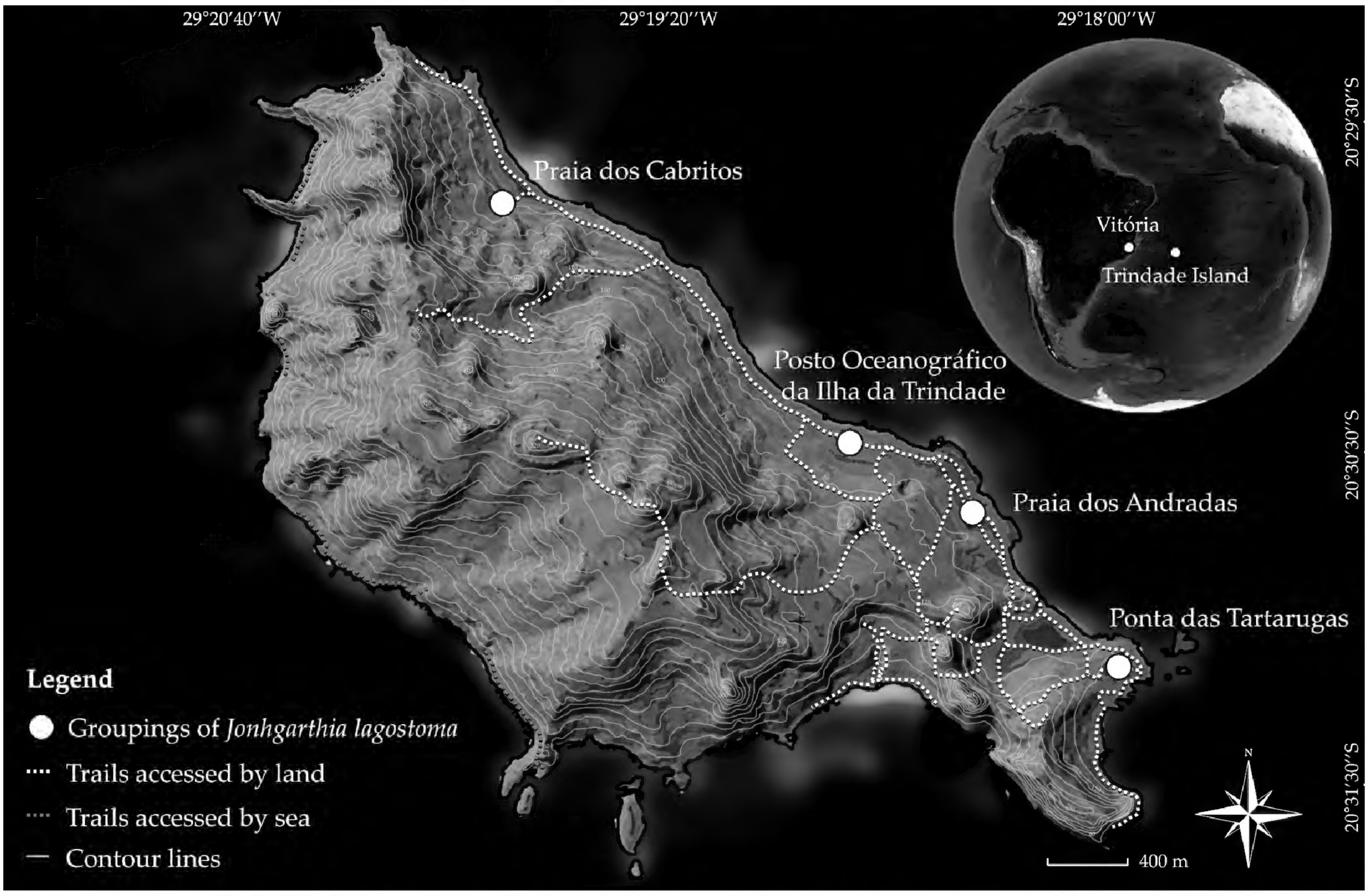

Figure 1. Trindade Island in the South Atlantic Ocean with the location of sampled trails and the distribution of the non-breeding groupings of *Johngarthia lagostoma* (H. Milne Edwards, 1837).

tion, elevation of the terrain, characteristics of the environment (e.g., presence of vegetation, proximity to watercourses, type of substrate, availability of food) and behavior of specimens (foraging or breeding) were noted. For isolated individuals, only general aspects of the environment (e.g., rocky substrate and/or vegetated site) were observed.

Chromatic variation

Groupings were also analyzed considering the color of the individuals' cephalothorax for chromatic characterization of the population. For this, each individual was classified qualitatively, based on photography, as yellow (also considering orange individuals), purple and intermediate (predominantly yellow with large purple patches on the carapace; according to the classification proposed by Hartnoll et al. 2009) (Fig. 2A). Then, we calculate the percentage of individuals at each color category. To confirm the chromatic pattern of the studied population, the results were compared with those found by João et al. (2021) (data collected during the reproductive period, between December 2019 and February 2020) on Trindade Island using G-test of independence with William's correction. For comparison between populational units, the results obtained in this study and by João et al. (2021) were added to represent the population of Trindade Island. Next, Trindade Island was compared with Atol das Rocas (based on data available in Teixeira 1996) and Ascension Island (based on data available in Hartnoll et al. 2009) (Fig. 3A). Particularly for Ascension Island, only individuals classified as yellow and purple were considered, as Hartnoll et al. (2009)

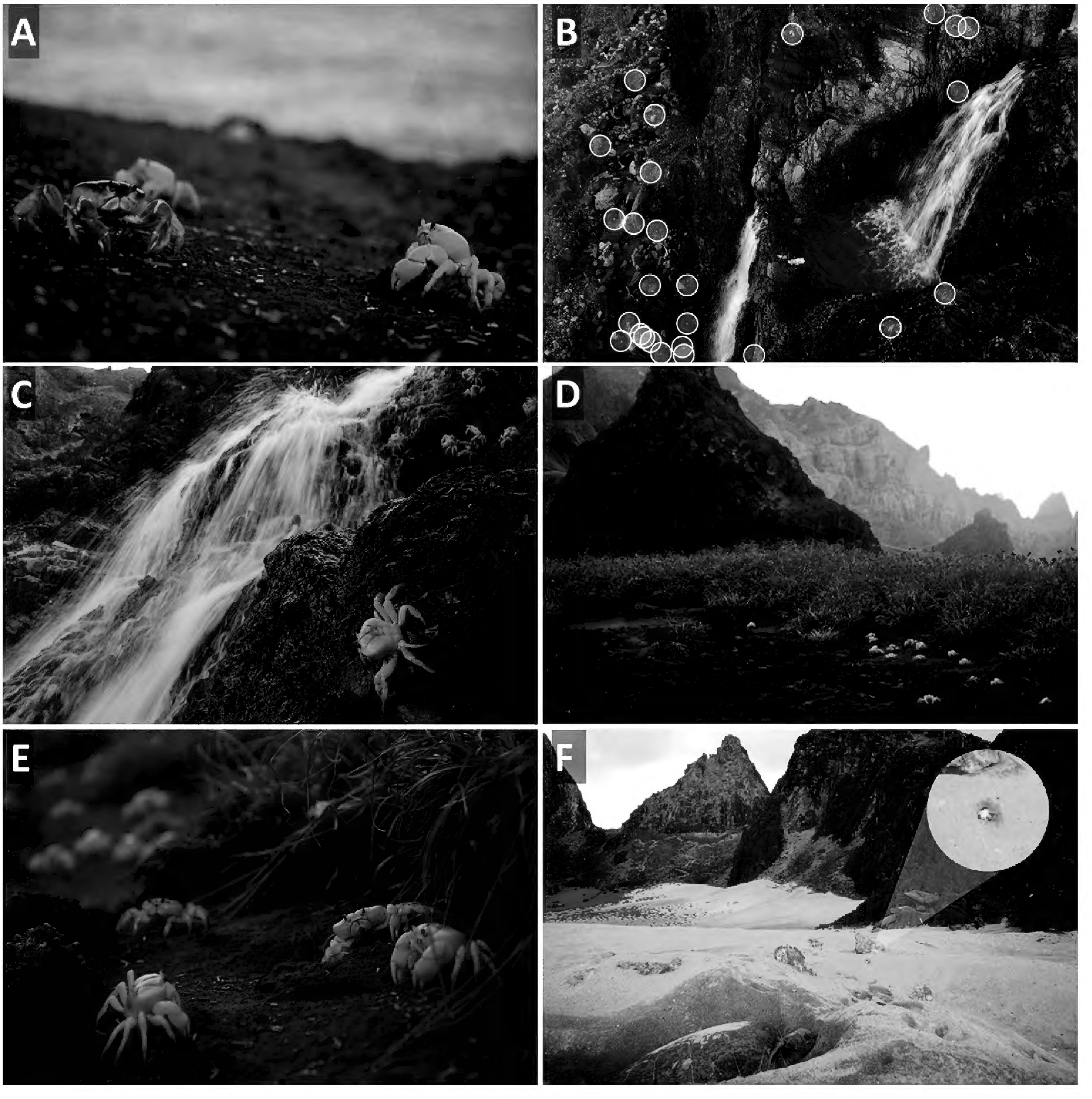

Figure 2. Purple (left) and yellow (right) individuals of *Johngarthia lagostoma* (H. Milne Edwards, 1837) recorded in Trindade Island (**A**). Grouping *J. lagostoma* recorded in a watercourse (**B**), with detail of individuals in foraging activity (**C**). Soil exposed by intense grazing of *Cyperus atlanticus* Hemsl. by the species (**D** – lower portion), with detail of the rhizomes of consumed plants, accumulation of feces and individuals near burrows (**E**). Consumption of a newly hatched individual of *Chelonia mydas* (Linnaeus, 1758) (**F**). Photographs by Hilton Entringer Jr.

were the only ones that presented individuals classified in the intermediate color category. The chromatic pattern of each population was determined by the predominance of individuals from one color category (Chi-square test with Yates' correction) and then the chromatic pattern was compared between populations (G-test). Finally, the Euclidean distance was calculated using the percentage of individuals in each color category to indicate the level of dissimilarity in the chromatic pattern between populations, with 0 representing the minimum distance (equal pattern). The analyses described were performed using the BioEstat software (Version 5.3; Ayres et al. 2007).

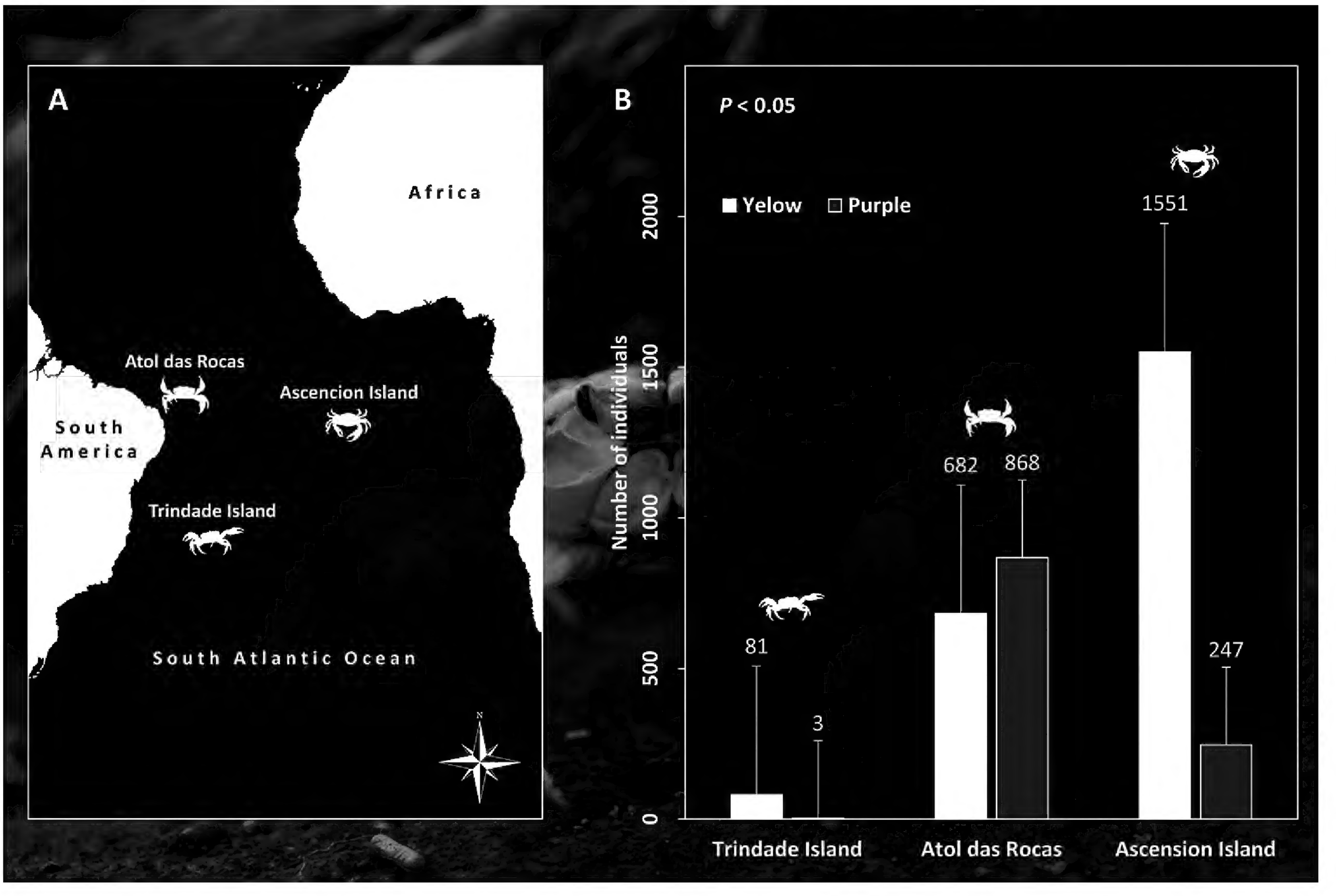

Figure 3. Location of *Jhongarthia lagostoma* (H. Milne Edwards, 1837) populations studied in the South Atlantic Ocean (**A**) and chromatic variation between yellow and purple individuals (**B**). Error bars represent ± SE (χ^2_{Yates}, $\alpha = 0.05$).

Results

Habitat use

J. lagostoma was observed along most of the trails. Isolated individuals were commonly recorded in rocky environments with little vegetation or non-vegetated sites dispersed throughout the island and distributed in almost all altitudinal ranges sampled (~ 570 m of maximum sampled altitude). Groups were observed in four locations, which differed from the physiognomic arid matrix. At "Praia dos Cabritos", visited in mid-April and late May, a group was observed on rocky and wet substrate along a watercourse next to a turtle breeding area (alt. ~ 30 m; Figs 1, 2B, C). At "Ponta das Tartarugas", visited once in June, the individuals were on a hill with unconsolidated substrate, where there were many burrows of the species and traces of intense consumption of the endemic grass *Cyperus atlanticus* Hemsl., resulting in soil exposure (alt. ~ 34 m; Figs 1, 2D, E). Close to the "Ponta das Tartarugas", in "Praia das Tartarugas" (main turtle spawning area on Trindade Island), the consumption of eggs and the predation of hatchlings of *Chelonia mydas* (Linnaeus, 1758) by *J. lagostoma* were observed (alt. ~ 2 m; Fig. 2F). At "Praia dos Andradas", visited daily, the group were observed in an herbaceous field dominated by *Canavalia obtusifolia* (Lam.) and *Ipomea* spp. throughout the sampled period, and the consumption of these plants

was also observed, with a relatively high number of burrows under the sandy and organic soil (alt. ~ 6 m; Fig. 1). In addition, "Praia dos Andradas" is also among the main beaches used by sea turtles for reproduction, and there were eggs and chicks available in the sampled period. At POIT, where there were *Terminalia catappa* L. trees (exotic species cultivated on the island), the grouping was also recorded daily, with the existence of burrows and consumption of nuts and leaves of *T. catappa*, in addition to food supplied and waste discarded by humans (alt. ~ 12 m; Fig. 1). It is also worth mentioning that the capture of individuals for human consumption during the sampling period was observed in the vicinity of the POIT. All groups recorded were characterized by foraging activity, with no evidence of reproductive activity.

Chromatic variation

Two groups had the chromatic variation of the individuals evaluated. The first one was located at "Praia dos Cabritos", and from the total number of individuals counted (n = 23), 22 (95.6%) were yellow and one (4.4%) was classified as purple. In the second grouping, located in "Ponta das Tartarugas", 21 individuals were evaluated, 20 (95.2%) of them were categorized as yellow and only one (4.8%) was purple. In total, 44 individuals were evaluated, most of them yellow (95.4%). The chromatic pattern of individuals did not differ from that observed by João et al. (2021) ($G_{Williams}$ = 0.223; g.l. = 1; P = 0.636), whose yellow color was also predominant (n = 39; 97.5%) compared to purple individuals (n = 1; 2.5%). This result indicates that the chromatic pattern observed in 2015 was maintained by the population at least until 2019–2020. Considering the total number of individuals evaluated on Trindade Island (n = 84), the yellow chromatic pattern was predominant in the population (χ^2_{Yates} = 70.583; g.l. = 1; P = 0.000; Table 1, Fig. 3B). Regarding the chromatic pattern in the other populational units, Atol das Rocas presented a predominance of purple individuals (χ^2_{Yates} = 22.081; gl = 1; P = 0.000; Table 1, Fig. 3B) and in Ascension Island the yellow individuals were the majority (χ^2_{Yates} = 944.276; gl = 1; P = 0.000; Table 1, Fig. 3B). In general, the populations units showed different chromatic patterns from each other ($G_{Williams}$ = 738.023; gl = 2; P = 0.000, Fig. 3B), and Trindade Island and Ascension Island are more similar to each other (Euclidean distance: 0.629), than both of them in relation to Atol das Rocas (Euclidean distance – Trindade Island = 3.265; Ascension Island = 2.635).

Table 1. Chromatic variation among the three populational units of *Johngarthia lagostoma* (H. Milne Edwards, 1837) in the South Atlantic Ocean.

Populations	Number of individuals			% of individuals	
	Total	Yellow	Purple	Yellow	Purple
Trindade Island[a]	84	81	3	96.4	3.6
Atol das Rocas[b]	1550	682	868	44.0	56.0
Ascension Island[c]	1798	1551	247	86.3	13.7

[a] Trindade Island data compiled; [b] Teixeira 1996; [c] Hartnoll et al. 2009.

Discussion

The habitat use by *J. lagostoma* on Trindade Island may have been influenced by availability of food resources and more adequate habitat conditions (sediment suitable for shelters construction, humidity and shade), and these factors may also have induced the formation of groupings during non-breeding periods. In its turn, the color patterns differed between populations and can be attributed to the founder effect, highlighting genetic populational differences.

Regarding the influence of resources on the spatial organization of the species, it is noteworthy that, when the distribution of resources is irregular, it is expected that the activity of the species is concentrated in places more favorable to obtaining resources (Stephens et al. 2007). In addition to offering food resources, suitable sites for *J. lagostoma* should also contain substrate that favors the construction of shelters and that are more humid and associated with vegetation that provides shade (Hartnoll et al. 2006). Similarly, João et al. (2021) reported that *J. lagostoma* is distributed in different types of habitat, although it is more abundant in vegetated sandy areas and adjacent sandy beaches, being also observed in rocky escarpments and in the highest points of Trindade Island. Thus, we suggested that the occasional occurrence of non-breeding groups may be a result of the irregular and reduced availability of favorable environments for the maintenance of individuals amidst the rocky matrix and with scarcity of resources. Furthermore, the grouping in specific locations on the island, the isolated and spaced individuals in most of the trails and the absence of records in more inhospitable places indicate a heterogeneous distribution of *J. lagostoma* in Trindade Island. Such observations also offer more detail about the previous reports that the species would be abundant on the entire island (Alves 1998; Alves and Silva 2016).

Habitat use and group formation by *J. lagostoma* on Trindade Island may have been influenced by the spatial distribution of food resources, such as sea turtle eggs and hatchlings, plants and waste discarded by humans. In our study, three of the four groupings were recorded near the main nesting beaches of *C. mydas* (except POIT grouping). This suggests that the use of space by *J. lagostoma* could be influenced by the reproductive activity of migratory species. Eggs and hatchlings of *C. mydas* can represent an important source of food and induce a more intense use of certain areas, with consumption of the species observed in Trindade Island, Fernando de Noronha and Atol das Rocas (Bellini and Sales 1992). Data collected after our sample period show that the beaches of Trindade Island attract crabs that take advantage of the resource provided by turtles (Oliveira 2021), which was also observed in the present study, although the sampling was carried out near the end of the reproductive period of these reptiles. On Trindade Island there are also records of predation of *J. lagostoma* on *Pterodroma arminjoniana* (Giglioli & Salvadori, 1869) (Luigi et al. 2009), *Sula dactylatra* (Lesson, 1831) and *Onychoprion fuscatus* (Linnaeus, 1766) (Teixeira et al. 1991), and the use of areas where seabird breeding occurs can also become more intense when eggs and chicks are available, as noted

on Ascension Island (Hartnoll et al. 2006). In addition to highlighting the importance of the animal resource in the use of space by *J. lagostoma*, the data presented also show the importance of the species as a predator of different zoological groups.

In addition to the consumption of animals, the consumption of native plants, such as *C. atlanticus*, *C. obtusifolia* and *Ipomea* spp., and exotic plants, such as *T. catappa*, was also recorded. Plant items are also consumed and may be important for other species of *Johngarthia*, such as omnivores and opportunists *J. malpilensis*, which regularly consume microalgae obtained from rocky surfaces, in addition to bird droppings and feathers (López-Victoria and Werding 2008), and *J. planata*, consuming vascular plants and litter (Vargas 2015). In the present study, the intense grazing of *C. atlanticus* was recorded, and its consumption can be complementary to the resource of animal origin, according to Oliveira (2021). However, it is considered that *C. atlanticus* may represent an even more important resource, since a large extension of grazed soil, accumulation of burrows and groups of individuals were associated with one of the places where the grass occurs. Furthermore, unlike migratory species that represent an important source of resource during their respective reproductive periods, *C. atlanticus* and other plants are continuously available and, therefore, can represent a key resource in periods with lower availability of animal protein. Thus, it is noteworthy that the maintenance of *J. lagostoma* may depend also on the availability of plant resources and, on the other hand, this crab can contribute to the control of insular vegetation from its direct consumption.

Beyond the groupings registered in places with less anthropogenic influence, there were also groups recorded in the POIT. Areas inhabited by humans can favor the presence of *J. lagostoma* when they offer adequate resources and conditions for the species. On Ascension Island, the Georgetown city gardens, where the soil is irrigated and vegetation is cultivated, is frequently used by the species (Hartnoll et al. 2006). At POIT, the availability of *T. catappa* is high, providing shade and food, and human food scraps are intentionally available to the crabs, promoting the frequent agglomeration of individuals, especially next to the restaurant. We highlight that the specimens also consume inert material (e.g., plastic), and there should be a better waste management on Trindade Island.

All groupings recorded on Trindade Island were located at altitudes below 40 m, while isolated individuals were observed in all altitudinal ranges, including the highest areas of the island (> 500 m). The species also occupies different altitudinal ranges on Ascension Island (max. alt. 859 m; Manning and Chace 1990; Hartnoll et al. 2006), including enclaves of suitable environments amidst the arid matrix in low altitudinal areas (< 50 m) or in forest habitat in higher altitudinal areas (> 200 m; Hartnoll et al. 2006). Individuals can also occur together and remain in these locations during the non-breeding period (Hartnoll et al. 2006). This suggests that there is the formation of non-breeding groups also on Ascension Island and that suitable areas may house a higher density of individuals regardless of the altitude. In addition, habitat use may also differ along the species' biological cycle, as rocky and unvegetated areas are used only during the breeding periods to access the sea on

Ascension Island (Hartnoll et al. 2009). These characteristics may be shared among other *Johngarthia* species, with *J. planata* (Stimpson, 1860) also being more associated with vegetated habitats (Perger 2019), while *J. malpilensis* (Faxon, 1893) occurs at different altitudes, but in greater density where there is available organic and unconsolidated soil (López-Victoria and Werding 2008).

Since the environments of Trindade Island have been historically and profoundly altered, we suggested that the current distribution of *J. lagostoma* may be different from the original. The same can be proposed for the other islands, since the species is restricted to a small area in Fernando de Noronha (Serafini et al. 2010) and to specific areas in Ascension Island (Hartnoll et al. 2006). These islands also show significant environmental changes and populations of *J. lagostoma* are currently reduced (Hartnoll et al. 2006; Serafini et al. 2010). Furthermore, the anthropic consumption of individuals may also have contributed to the reduction of populations of *J. lagostoma*, since this activity can also impact other populations of the species (e.g., Lira 2017). Additionally, due to low connectivity between populations, slow population growth and irregular recruitment (AIG 2015), the species may become more vulnerable to extinction (Pinheiro et al. 2016). Considering this, special attention should be given to the population of *J. lagostoma* on Trindade Island, where its consumption by humans occurs and there are no guidelines for the conservation of the species (Personal Observation).

The chromatic pattern differed between populations, with Trindade Island and Ascension Island more similar to each other (predominance of yellow individuals) and more different in relation to Atol das Rocas (smaller difference between the color categories, but with more purple individuals). The variation in the chromatic pattern reflects the genetic structure observed for each populational unit, and it varies between the evaluated locations (Rodríguez-Rey et al. 2016). Since the genetic structure of island populations is determined by a fraction of the genetic diversity present in the population of origin (e.g., Frankham 1997), the dissimilarity in the chromatic pattern of *J. lagostoma* can be attributed to the founder effect. This factor may also have resulted in low local genetic variability and in the differentiated genetic pattern between populations, with the populations of Trindade Island and Ascension Island originated from individuals from Atol das Rocas (Rodríguez-Rey et al. 2016). Thus, we suggested that the chromatic patterns of Trindade Island and Ascension Island may have been produced (1) by the more frequent entry of individuals with certain characteristics originating from the Atol das Rocas in the past and (2) by the possible eventual dispersion of larvae between Trindade Island and Ascension Island. We also suggest that the populations be evaluated for possible temporal variations in the chromatic pattern, which can help in determining the environmental and biological factors that can generate such variation. Until these issues are not resolved, due to the relationship between genetic structure and chromatic pattern, we propose that populations should be considered as individual management units.

Conclusions

According to the data presented, the conservation of localities with characteristics favorable to the establishment of the species, individually or in groups, is essential for the maintenance of the population of *J. lagostoma* on Trindade Island, a key species in the insular trophic chain. Therefore, we suggest that the maintenance of natural food resources and native vegetation, as well as stimulating plant restoration, can contribute to the maintenance of the studied population. We also highlight the need to reduce threats that contribute to populational decline, such as the anthropogenic consumption of these crabs, which should be effectively prohibited in Trindade Island. These actions can benefit the species in general, as it is restricted to a few isolated islands, many of which have had their terrestrial environment significantly impacted after human colonization.

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